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Effects of elevation and land use on the biomass of trees, shrubs and herbs at Mount Kilimanjaro

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Abstract. The protection and sustainable management of forest carbon stocks, particularly in the tropics, is a key factor in the mitigation of global change effects. However, our knowledge of how land use and elevation affect carbon stocks in tropical ecosystems is very limited. We compared aboveground biomass of trees, shrubs and herbs for eleven natural and human-influenced habitat types occurring over a wide elevation gradient (866–4550 m) at the world's highest solitary mountain, Mount Kilimanjaro. Thanks to the enormous elevation gradient, we covered important natural habitat types, e.g., savanna woodlands, montane rainforest and afro-alpine vegetation, as well as important land-use types such as maize fields, grasslands, traditional home gardens, coffee plantations and selectively logged forest. To assess tree and shrub biomass with pantropical allometric equations, we measured tree height, diameter at breast height and wood density and to assess herbaceous biomass, we sampled destructively. Among natural habitats, tree biomass was highest at intermediate elevation in the montane zone (340 Mg ha^{-1}), shrub biomass declined linearly from 7 Mg ha^{-1} at 900 m to zero above 4000 m, and, inverse to tree biomass, herbaceous biomass was lower at mid-elevations (1 Mg ha^{-1}) than in savannas (900 m, 3 Mg ha^{-1}) or alpine vegetation (above 4000 m, 6 Mg ha^{-1}). While the various land-use types dramatically decreased woody biomass at all elevations, though to various degrees, herbaceous biomass was typically increased. Our study highlights tropical montane forest biomass as important aboveground carbon stock and quantifies the extent of the strong aboveground biomass reductions by the major land-use types, common to East Africa. Further, it shows that elevation and land use differently affect different vegetation strata, and thus the matrix for other organisms.

Key words: carbon stock; elevation gradient; land-use change; tropical mountain; vegetation strata.

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INTRODUCTION

Tropical forests are estimated to harbour some 25% of the terrestrial biosphere's carbon (Bonan 2008). They play a key role in ecosystem carbon sequestration and hence, for climate change mitigation (Malhi and Grace 2000, Lewis et al. 2004, Houghton 2007). While there is substantial

evidence that primary tropical forests are a carbon sink, large uncertainties exist regarding the size of standing stocks and the impacts of human land use on them, especially in Africa (Houghton 2007, Lewis et al. 2009, Pan et al. 2011). These uncertainties prevent effective estimates of anthropogenic carbon losses when deforestation and land use occur. Such estimates, however, are essential to conserve and sustainably manage tropical forest carbon stocks, e.g., in programs for the reduction of emissions due to deforestation and degradation (REDD+; Gibbs et al. 2007).

Local forest inventories are lacking for various regions and habitat types, including tropical montane ecosystems, for which the relationship between elevation and carbon stocks is poorly characterised (Houghton 2005, Spracklen and Righelato 2013). Previous studies of tropical montane biomass stocks have been conducted in tropical Asia (Kitayama and Aiba 2002, Culmsee et al. 2010), South America (Alves et al. 2010, Girardin et al. 2010, Moser et al. 2011) and East Africa (Marshall et al. 2012). In most of these studies, carbon stocks decreased with elevation, while carbon stocks at a given elevation varied strongly between and within continents. This pattern is likely to be driven by differences in climate. However, other environmental parameters, such as soil nutrient availability, also play a role, and general patterns still need to be identified (Malhi et al. 2006, Slik et al. 2010, Spracklen and Righelato 2013). Also, most studies did not consider shrub or herb biomass, whose importance relative to trees is therefore poorly known.

Land-use change, particularly deforestation, contributes importantly to the land-atmosphere carbon flux (Foley et al. 2005, Houghton 2007, Ramankutty et al. 2007). In tropical Africa, the carbon emissions from land-use change exceed those from fossil fuel combustion (Canadell et al. 2009) and future land-use change might further deplete carbon stocks, as some land-use types still store significant amounts of carbon (Albrecht and Kandji 2003, Kumar and Nair 2011). However, accurate estimates of land-use change effects on carbon stocks are not available for many tropical habitats and the effect of land use on woody and non-woody vegetation strata has not been quantified. This makes it difficult to predict how ecosystem carbon budgets will respond to future changes (Gibbs et al. 2007, Houghton 2007).

Here we study the aboveground biomass (hereafter biomass) of natural and anthropogenically affected tropical habitat types at different elevations at Mt. Kilimanjaro, Tanzania. Mt. Kilimanjaro is the world's highest free-standing mountain and harbours a wide range of different habitat types, including savanna woodlands, mountain cloud forest and afro-alpine vegetation. Its vegetation has been strongly influenced by human impacts and there is considerable variation in land-use types and intensities across the mountain (Agrawala et al. 2003, Hemp 2006*a*). We measured the biomass of three vegetation strata (tree, shrub and herbaceous layer) in six important major natural habitat types and five anthropogenically affected types over an elevation range of 3680 m from the savanna to the afro-alpine zone based on forest inventories and destructive herbaceous biomass sampling. Because tree architecture varies strongly between habitat types as different as tropical rainforest and savannas, we used different allometric equations to adequately estimate tree and shrub biomass from our forest inventory data. We asked how biomass of natural habitats is distributed along the elevation gradient and how anthropogenic influence modulates the biomass at different elevations.

Methods

Study system and design

We studied the southern and south-eastern slopes of Mt. Kilimanjaro, where climate gradients are most pronounced and various habitat types are present. Mean annual temperature ranges from about 23°C at 800 m a.s.l. in the savanna to −7°C at 5895 m at Uhuru-peak (Hemp 2006*b*). Precipitation also strongly changes with elevation with dry foothills and afro-alpine heathlands, and a mid-elevational precipitation peak at around 2200 m (Hemp 2006*b*). An optimum for biomass production may thus be expected at medium elevations, where precipitation is high, but temperatures are not too low to constrain growth considerably.

The following important natural and anthropogenically used habitat types occur at the

mountain and were investigated in our study: In the foothills of the mountain from 800 to 1100 m, savanna woodlands with *Acacia-Commiphora* vegetation dominate the natural landscape. However, these woodlands are increasingly transformed into maize fields for local and regional food production.

In the densely populated lower-montane area between 1200 and 2000 m, patches of lower montane forest represent the natural vegetation and three major land-use types are found in this elevation zone. The traditional agricultural system of the local Chagga people, the "Chagga home gardens", is by far the most abundant. The Chagga people use these multi-layered gardens to grow different crops such as bananas, coffee, avocados, taro and beans, keeping forest trees for shade (Hemp 2006*a*). The second land-use type is grasslands, which are cut frequently by the Chagga people to obtain fodder for their livestock. More recently, commercial coffee plantations have spread on the southern slope of Kilimanjaro. These plantations mostly cover quite large and homogeneous areas with scattered, often non-native, trees.

The natural montane *Ocotea* forest grows between 2100 and 2800 m and is dominated by the camphor tree (*Ocotea usambarensis*, Lauraceae), which was also the main target of commercial selective logging activities until 1984 (Agrawala et al. 2003). The legacy of this forestry is seen in *Ocotea* forests disturbed by selective logging.

Above 2800 m, the gymnosperm *Podocarpus latifolius* (Podocarpaceae) dominates the upper montane *Podocarpus* forest up to about 3100 m. In the subalpine zone, up to 4000 m, patches of natural *Erica* forest dominated by *E. trimera* represent remnants of Africa's highest forests. Finally, in the alpine zone up to 4500 m, cushion plants of the genus *Helichrysum* dominate together with tussock grasses.

Across the slope, plots were established in the 11 habitat types described above so that the most important primary and human dominated habitats were represented (Hemp 2006*b*). Each habitat type was replicated five times, resulting in 55 plots for this study. Each plot was 0.25 ha in size, except for savanna plots, which were one hectare in size on account of their low tree density. Plot boundary positions were recorded with GPS and permanently marked with subterranean iron nails. For each plot, mean annual temperature (MAT) was obtained from in-situ measures by temperature loggers (data logger DK320, Driesen and Kern GmbH, Bad Bramstedt, Germany) and mean annual precipitation (MAP) was modeled using long-term observations based on a 15-year dataset from a network rain gauges distributed across the whole mountain (Appelhans et al. 2014; see also Appendix A for further details on habitat types and plot characteristics).

Measurements

Tree inventory.—Within each plot, all trees wider than 10 cm diameter at breast height (dbh) were marked with aluminium tags and their dbh and height were measured. The dbh was measured with a diameter tape (Forestry Suppliers, USA) at 1.3 m for normally shaped trees and 20 cm below or above when branches or irregular shapes impeded measurement at that height. The 1.3 m height was measured from the highest ground level around the stem to standardize measurements taken on slopes. For trees which were strongly buttressed or too big to measure by hand, a laser dendrometer (Criterion RD 1000 with TruPulse 200/200, Centennial, USA) was used to measure the tree above the buttresses and at 1.3 m. Lianas above 10 cm in diameter were also marked and their dbh was measured. Tree height was measured using an ultra-sonic hypsometer (Vertex IV Hypsometer, Haglöf, Langsele, Sweden) or a laser rangefinder (TruPulse 200/200). The tree inventories were carried out between December 2010 and March 2013 for all plots containing trees except for the five plots in the subalpine *Erica* forest, where we only studied herbaceous biomass.

Shrub inventory.—The shrub inventory was carried out within a 5×20 m subplot in the centre of each plot. Within this subplot, the shrub layer was defined as consisting of all woody stems exceeding 1.3 m in height, but below 10 cm dbh and thus not included in the tree inventory. We measured dbh at 1.3 m with a diameter tape (Forestry Suppliers; for dbh's above 3 cm) or a caliper (for dbh's below 3 cm) and the height of each shrub with a hypsometer.

Herbaceous biomass collection.—For the herbaceous biomass, four 0.25-m^2 samples per plot

Table 1. Allometric equations used for the different habitat types and plant groups.

Type	Allometric equation	Reference	Plots
Savanna	$AGB = 0.0763 \times dbh^{2.2046} \times H^{0.4918}$	Mugasha et al. 2013	Savanna Maize fields
Wet forest	$AGB = \exp(-2.557 + 0.940\ (\ln(wd \times dbh^2 \times H)))$	Chave et al. 2005	Low. montane forest Home gardens (1, 3) Coffee plantations (2) *Ocotea* forest Select. logged forest *Podocarpus* forest
Dry forest	$AGB = \exp(-2.187 + 0.916\ (\ln(wd \times dbh^2 \times H)))$	Chave et al. 2005	Home gardens (2, 4–5) Coffee plant. (1, 3–5) Grasslands
Lianas	$AGB = \exp(-1.484 + 2.657\ (\ln(dbh)))$	Schnitzer et al. 2006	Low. montane forest *Ocotea* forest Select. logged forest
Bananas	$AGB = 0.03 \times dbh^{2.13}$	Hairiah et al. 2010	Home gardens Coffee plantations
Coffee	$AGB = 0.281 \times dbh^{2.06}$	Hairiah et al. 2010	Home gardens Coffee plantations

Notes: Type denotes the habitat type for which equations apply for, according to their authors. Plots denotes the types of habitat (and for home gardens and coffee plantations also the exact plots in parentheses) for which the equations were used in our study. Measured parameters used in the equations were total plant height (H), diameter at breast height (dbh) and wood density (wd, measured as dry weight divided by fresh volume). For a detailed description of the choice of the equations, see Appendix B.

were taken non-randomly from areas were the herbaceous layer was considered as being representative of the whole plot. The biomass of the herbaceous layer (hereafter herbaceous biomass) included forbs with a woody stem, mosses and lichens, which were collected from ground level using a wooden frame of 50×50 cm and scissors. Samples were dried in a drying oven at 72°C for 72 hours and then weighed. In habitat types with pronounced rainfall seasons (savanna, maize fields, grasslands, coffee plantations, home gardens), biomass was collected after the wet season maximum, in December and January 2010–2011, while in the maize plots, it was collected in June and July 2012, shortly before the harvest. The other samples were collected between December 2010 and October 2012. This allowed us to estimate the maximum standing biomass of the herbaceous layer on each plot.

Wood density.—Wood density was measured as dry weight divided by fresh volume for field-collected wood cores (Increment borer 50 cm, Suunto, Vantaa, Finland) of the dominant tree and shrub species accounting for 80% of the ground cover of all trees and shrubs in each plot, i.e., for 66 of a total of 132 identified species. Wood cores were taken from at least five individuals, if possible from different sites, at 1.3 m height and samples were oven dried at 72°C for at least 72 hours and weighed under exclusion of any remoistening (in sealed boxes with silica gel). Wood density values for the remaining 66 species were taken from the global wood density database (Zanne et al. 2009). When species-level data was not available or species identification was not possible (110 out of 4500 stems), mean genus-level values were used and family-level means were applied when the genus-level data was not available or when an individual could not be identified to genus level (74 out of 4500 stems). If an individual could not be identified at all (250 out of 4500 stems), mean plot values were used (Marshall et al. 2012).

Allometric equations

The choice of an appropriate allometric model is the crucial step towards minimizing the errors in forest biomass estimates (Chave et al. 2004, Molto et al. 2013). Therefore, we carefully chose the allometric equations most suited for the 4500 stems measured in the different habitat types so as to acquire the best possible approximation of their aboveground biomass (Table 1; Appendix B). For the forest habitats and lower montane land-use plots, we used pantropical equations for trees, shrubs and lianas developed by Chave et al. (2005) and by Schnitzer et al. (2006), which were specifically developed for use outside their sample range and were shown to produce

Table 2. Biomass and total carbon stock (mean with SE in parentheses) of 11 important habitat types (Type) at Mount Kilimanjaro.

Zone	Type	Biomass (Mg ha^{-1})				Total carbon (Mg C ha^{-1})
		Herbs	Shrubs	Trees	Total	
Savanna	**Savanna**	2.5 (0.6)	4.4 (1.3)	3.5 (1.0)	10.4 (2.1)	5.1 (1.0)
	Maize field	15.2 (2.9)	0.6 (0.6)	0.8 (0.7)	16.6 (2.4)	8.0 (1.2)
Lower montane	**Natural forest**	0.9 (0.3)	4.7 (1.0)	355.4 (89.0)	361.1 (88.8)	174.0 (42.8)
	Home garden	0.7 (0.2)	22.8 (3.6)	69.8 (17.0)	93.2 (17.2)	44.9 (8.3)
	Coffee plantation	1.6 (0.4)	9.4 (5.8)	46.9 (22.3)	57.9 (22.1)	27.9 (10.7)
	Grassland	2.9 (1.1)	0.1 (0.1)	0.6 (0.3)	3.5 (1.0)	1.7 (0.5)
Montane	***Ocotea* forest**	1.1 (0.1)	6.0 (1.8)	274.4 (47.2)	281.6 (48.9)	135.7 (23.6)
	Logged forest	1.3 (0.2)	9.1 (4.0)	347.5 (19.0)	357.9 (22.1)	172.5 (10.6)
Upper montane	***Podocarpus* forest**	4.0 (1.5)	1.8 (1.1)	364.9 (6.1)	372.3 (4.3)	179.5 (2.1)
Subalpine	***Erica* forest**	8.8 (2.1)	...	...	...	...
Alpine	***Helichrysum* zone**	6.3 (2.1)	0 (0)	0 (0)	6.3 (2.1)	3.1 (1.0)

Notes: Biomass is given for the herbaceous (Herbs), shrub (Shrubs) and tree layer (Trees) and as total. For definition of the different habitat types, elevation zones and sampling design, see *Materials and methods*. Natural habitats are in boldface. Mg C denotes total carbon (48.2% of total biomass; Thomas and Martin 2012).

reliable estimates for tropical forests and agricultural systems in Africa (Kuyah et al. 2012, Vieilledent et al. 2012, Fayolle et al. 2013). For bananas and pruned coffee shrubs, we opted for the equations developed by Hairiah et al. (2010). For the savanna, and for the maize fields with their occasional trees, we selected an equation recently developed by Mugasha et al. (2013), because it was specifically developed for dry woodlands in Tanzania (Table 1). A detailed description of the choice of the equations for each habitat type is given in the Appendix B. We added the biomasses per plot and upscaled them to values for one hectare. The carbon content of woody and herbaceous biomass was approximated as 48.2% (Table 2; Thomas and Martin 2012).

Statistical analyses

To analyze patterns of aboveground biomass in response to elevation and precipitation for the natural habitat types, we used linear regressions. We fitted linear, quadratic and cubic functions and selected the model with the lowest Akaike Information Criterion (AIC). To test for anthropogenic effects (natural versus human influenced habitat types) on biomass in each elevation zone, we used linear models. In these comparisons, we used plot elevation as a covariate.

When necessary, variables were log-transformed prior to the analyses. All analyses were performed using the lm library of R version 3.0.1 (R Core Team 2013).

Results

Biomass of natural habitats over elevation

Total aboveground biomass of natural habitats followed a clear unimodal pattern across the elevation gradient, peaking at around 2200 m in the montane *Ocotea* forest ($R^2 = 0.86$, $F_{1,19} = 6.6$, $P = 0.019$; Fig. 1). The highest biomass was found in one of the lower montane forest plots, which reached 664.3 Mg ha^{-1} (Appendix A). Total biomass decreased at both ends of the elevation gradient, reaching 10.4 Mg ha^{-1} in the savannas and 6.3 Mg ha^{-1} in the treeless, alpine *Helichrysum* vegetation. Precipitation explained a very similar amount of the variation in total biomass (Fig. 2; quadratic regression, $R^2 = 0.85$, $F_{1,20} = 28.2$, $P < 0.001$) as elevation did (Fig. 1; see above).

Trees contributed 33% to total biomass in the savanna, 98% in the forest and 0% in the alpine zone. Similar to total biomass, tree biomass showed a hump-shaped pattern across the elevation gradient ($R^2 = 0.89$, $F_{1,19} = 10.6$, $P = 0.004$; Fig. 1). Individual tree biomass values ranged from 0.002 Mg to a 24.4 Mg *Entandrophragma excelsum* tree in the lower montane forest. However, 88% of the trees weighed less than one ton and mean tree biomass was 0.6 Mg. The smallest tree biomass per plot was found in the savanna woodlands, with a mean of 3.5 Mg ha^{-1}.

Shrub biomass decreased significantly with elevation ($R^2 = 0.47$, $F_{1,21} = 20.6$, $P < 0.001$; Fig. 1). Fitting a quadratic function of shrub biomass

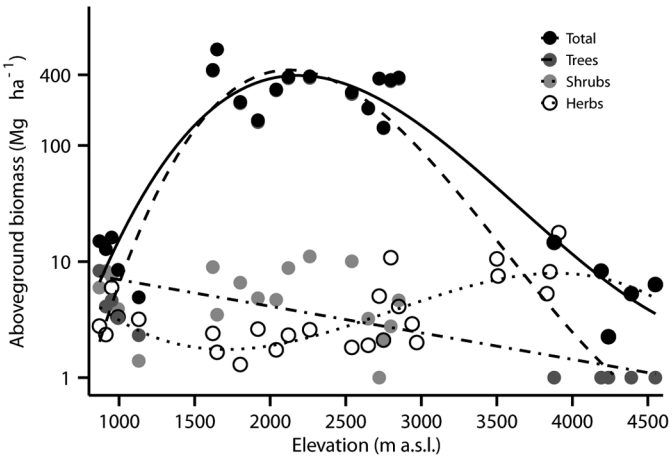

Fig. 1. Relationships of total (solid line), tree (dashed line), shrub (dash-dotted line) and herbaceous biomass (dotted line) of natural habitat types over the elevation gradient at Mount Kilimanjaro. Total biomass: cubic function = $R^2 = 0.86$, $F_{1,19} = 6.6$, $P = 0.019$, Trees: cubic function: $R^2 = 0.89$, $F_{1,19} = 10.6$, $P = 0.004$; Shrubs: linear function: $R^2 = 0.47$, $F_{1,21} = 20.6$, $P < 0.001$; Herbaceous: cubic function: $R^2 = 0.48$, $F_{1,26} = 10.7$, $P = 0.003$. Please note the log-scale.

with elevation explained a similar proportion of the total variation ($R^2 = 0.52$ for the quadratic versus 0.47 for the linear function), but did not improve the AIC. Shrub biomass exceeded tree biomass in the savanna (42% of total biomass), but made up only 1.3% of the total biomass in the lower montane rainforest, 2.2% in the montane *Ocotea* forest and 0.5% in the upper *Podocarpus* forests. The highest shrub biomass was found in a montane *Ocotea* forest plot with 10 Mg ha^{-1} (Appendix A).

In natural habitats herbaceous biomass showed bimodal pattern along the elevation gradient ($R^2 = 0.48$, $F_{1,26} = 10.7$, $P = 0.003$; Fig. 1), which was inverse to the hump shaped elevation pattern of tree biomass (reflecting a negative relationship between tree and herbaceous biomass: $F_{1,21} = 6.4$, $P = 0.02$). Herbaceous biomass contributed 24% of the total biomass in the savanna, 0.2% in the lower montane forest,

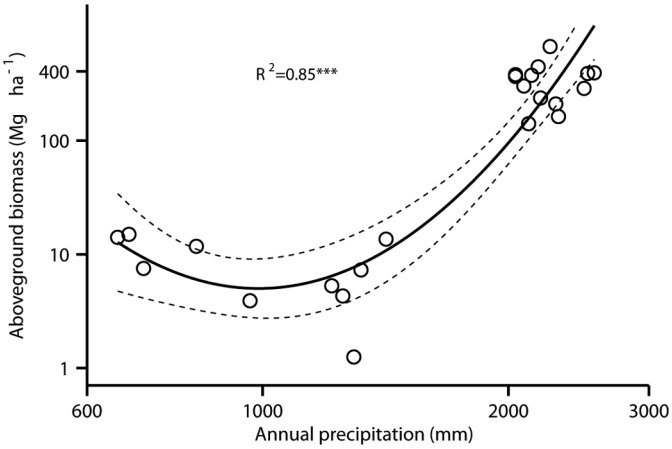

Fig. 2. Relationship between annual precipitation and total aboveground biomass per plot on a log-log scale for natural habitat types over the elevation gradient at Mount Kilimanjaro. Dashed lines indicate 95% CI. ***: $P < 0.001$.

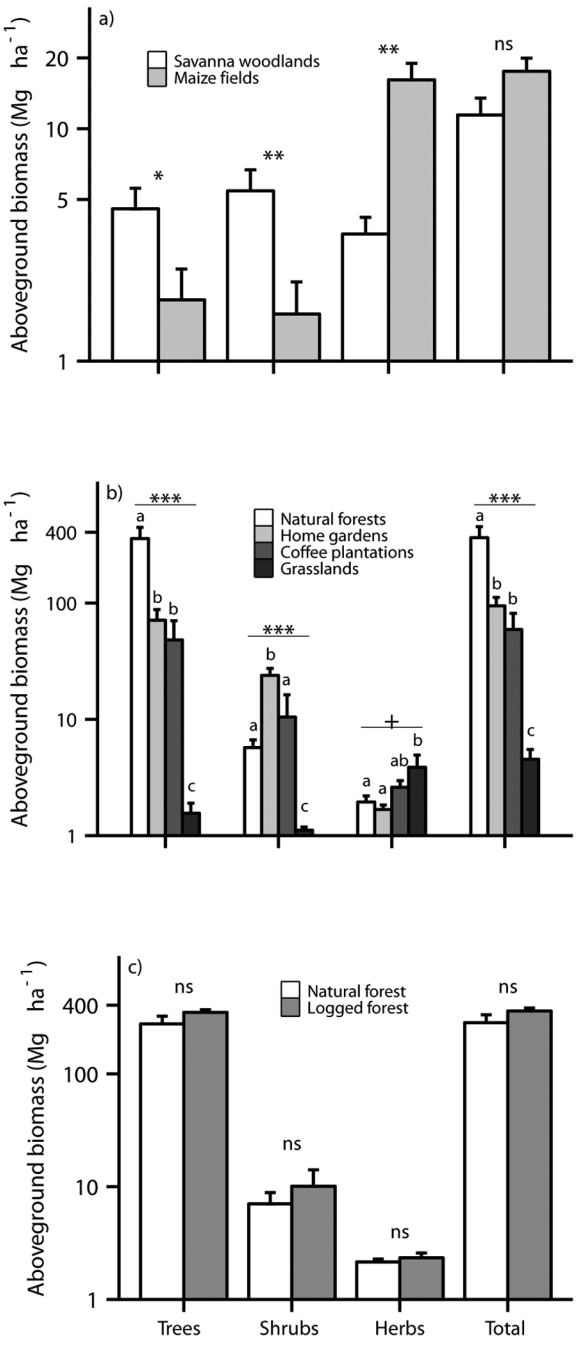

Fig. 3. Anthropogenic effects on biomass at different elevations at Mount Kilimanjaro, Tanzania. (a) Mean biomass of different vegetation strata (trees, shrubs, herbs and total (sum of all strata)) and standard errors for savanna woodlands and maize fields. (b) Mean biomass of different vegetation strata (trees, shrubs, herbs and total (sum of all strata)) and standard errors for lower montane forests, home gardens, coffee plantations and grasslands. Underlined asterisks indicate a significant habitat effect and letters indicate significant differences of pairwise comparisons of habitat types with a post-hoc test (Tukey's HSD). (c) Mean biomass of different strata (trees, shrubs, herbs and total (sum of all strata)) of natural and selectively logged montane *Ocotea* forests. +$P < 0.1$; *$P < 0.05$, **$P < 0.01$; ***$P < 0.001$ Please note the log-scale.

0.4% in the *Ocotea* forest, 1% in the upper montane *Podocarpus* forest and 100% in the treeless alpine vegetation (Fig. 1). The lower montane forests had the lowest herbaceous biomass of 0.9 Mg ha^{-1}. The highest herbaceous biomass was found in the subalpine *Erica* forest with up to 16.7 Mg ha^{-1}. The alpine *Helichrysum* vegetation above 4000 m still harboured substantial amounts of herbaceous biomass (mean 6.3 Mg ha^{-1}).

Anthropogenic effects on biomass at different elevations

In the savanna zone, while tree and shrub biomass were significantly lower in maize fields than in savanna woodlands (trees: $F_{1,7} = 8.75$, $P = 0.02$; shrubs: $F_{1,7} = 11.87$, $P = 0.01$), herbaceous biomass was more than 5-fold higher in maize fields than in savannas ($F_{1,7} = 32.91$, $P < 0.001$; Fig. 3a). As a result, total biomass did not differ between savanna woodlands and maize fields.

In the lower montane zone, total biomass strongly differed across the four different land-use types ($F_{3,12} = 8.44$, $P < 0.001$), declining strongly from natural forests to home gardens and coffee plantations and reaching its lowest value in grasslands, where it was 99% lower than in natural forests (Fig. 3b). While home gardens and coffee plantation stored more biomass than grasslands, they did not differ significantly from each other ($F_{1,7} = 1.4$, $P = 0.27$). Tree biomass followed the same pattern as total biomass (Fig. 3b). Shrub biomass also differed significantly across habitat types ($F_{3,12} = 41.03$, $P < 0.001$), but was significantly lower than in natural lower montane forests only in grasslands ($F_{1,7} = 43.07$, $P < 0.001$; Fig. 3b). Also, shrub biomass was higher in home gardens than in natural forest and coffee plantations, mainly due to the abundant bananas in the home gardens. The herbaceous biomass

did not differ between natural lower montane forests, home gardens and coffee plantations, but was higher in grasslands than in forests and home gardens (Fig. 3b).

In the montane *Ocotea* zone, selectively logged montane *Ocotea* forests did not differ from undisturbed ones in their tree, shrub, herbaceous and total biomass (Fig. 3c).

Discussion

Biomass of natural habitats over elevation

The distinct unimodal pattern in total and tree biomass over elevation coincided strongly with the precipitation pattern (Fig. 2), suggesting that precipitation is the main determinant of biomass variation at Mt. Kilimanjaro. This is in line with a meta-analysis across larger spatial scales (Stegen et al. 2011). Nevertheless, further drivers may modulate the precipitation effect on biomass, including soil nutrient relations or biotic interactions, such as herbivory (Stegen et al. 2011, Metcalfe et al. 2014).

Other studies on tropical mountains found a monotonous decrease of biomass with elevation rather than a unimodal pattern, e.g., in tropical Asia (Kitayama and Aiba 2002) and the Andes (Girardin et al. 2010, Moser et al. 2011), or even an increase (e.g., Culmsee et al. 2010, Marshall et al. 2012). However, in the cases where biomass decreased monotonously with elevation, the lowlands were not dryer than the higher elevations, contrasting with the precipitation pattern at Mt. Kilimanjaro. Moreover, the studies reporting an increase in biomass with elevation did not extend higher than 2500 m, and thus presumably did not exceed the tropical tree line.

In a remote sensing study, Willcock et al. (2012) approximated woody savanna biomass close to Mt. Kilimanjaro to 1–10 Mg ha^{-1}, which is congruent with our estimate of 7.9 Mg ha^{-1} for the combined mass of trees and shrubs. Other biomass studies of slightly more humid savanna ecosystems arrived at slightly higher estimates, e.g., 28–60 Mg ha^{-1} for the Miombo woodlands in southern Tanzania (Shirima et al. 2011) and 6.5–82.1 Mg ha^{-1} for savannas in South Africa (Colgan et al. 2012). The Miombo woodlands with twice the rainfall of the savannas surrounding Mt. Kilimanjaro are more forest-like with trees higher than 20 m, whereas Mt. Kilimanjaro's savanna trees are sparser and rarely exceed 8 m (10 out of 234 stems in our study). An additional reason for the comparatively low biomass of Mt. Kilimanjaro's savannas may be the high logging and burning pressure even for the savanna remnants studied here, which has intensified with the strong population increase in the region (Agrawala et al. 2003).

The lower montane forest zone at Mt. Kilimanjaro had the highest plot-level total biomass across the whole mountain, and also the highest variability between plots (SD of 198.5 Mg ha^{-1}). This was due to the patchy distribution of trees of >70 cm dbh, which comprised over 70% of tree biomass where present, as in a pantropical review (Slik et al. 2013). This patchy distribution of large trees may have been further increased by illegal timber and firewood cutting, which occurs more frequently in the lower montane forests due to their easier accessibility and proximity to the national park border just below.

Tree biomass remained high all the way up to the upper montane *Podocarpus* forest at 2800 m with a mean of 372 Mg ha^{-1} (Table 2). Other studies in high-altitude tropical regions report 129 and 112 Mg ha^{-1} at ~3000 m in the Andes (Girardin et al. 2010, Moser et al. 2011) and 210 Mg ha^{-1} in tropical Asia (Kitayama and Aiba 2002). This suggests that the general pattern found for lowland rainforests, according to which forest biomass is higher in Africa than in tropical America (Banin et al. 2012, Lewis et al. 2013, Slik et al. 2013), may also hold true for montane forests. The biomass of the upper montane *Podocarpus* forests on Kilimanjaro actually comes close to the estimates for African-wide lowland rainforest biomass (395.7 Mg ha^{-1}) compiled by Lewis et al. (2013). However, we are not aware of any other study investigating the biomass of African high montane forests; thus future studies need to confirm the generality of high carbon stocks in African upper-montane forests (Spracklen and Righelato 2013).

Shrub biomass was highest in the montane *Ocotea* forest with about 6 Mg ha^{-1} and differed strongly between habitat types. To date, few studies have separately estimated shrub biomass in tropical forests, especially along elevation gradients. E.g., Culmsee et al. (2010) found a slight increase of biomass of small diameter stems (between 2 and 10 cm dbh) with elevation,

which contrasts with our pattern (Fig. 1). In our study, herbaceous understorey growth was strong in the upper montane *Podocarpus* forests, where herbaceous vegetation reached heights of 2 m and more and exceeded the biomass of the shrub layer (Fig. 1). As these herbs compete with shrubs for light in the dark understorey, the strong herb layer might explain the relatively low shrub biomass in Mount Kilimanjaro's upper montane *Podocarpus* forests.

Herbaceous biomass was inversely related to woody biomass (Fig. 1), a pattern that seems largely due to reduced light availability under closed canopies. Thus, herbs only played a substantial role for total biomass production in habitats with low tree density.

The highest values of herbaceous biomass were found for subalpine *Erica* forest, reaching 16 Mg ha^{-1}. This may be due to the relatively open canopy of these forests, which allows for an extensive moss and lichen layer sometimes more than 20 cm thick. Few biomass estimates have been made for tropical alpine regions. In the South American Andes, biomass stocks of the Pàramo and Puna vegetation, where trees are also scarce, were reported between 6.7 and 7.4 Mg ha^{-1} (Gibbon et al. 2010, Oliveras et al. 2014). Our estimates of 6.3 Mg ha^{-1} for the alpine *Helichrysum* heaths are the first for afro-alpine vegetation.

Anthropogenic effects on biomass at different elevations

In the savanna zone, tree and shrub biomass was much lower in maize fields than in savannas, while the herbaceous biomass (i.e., crop biomass) was significantly higher, resulting in no net difference in total biomass (Fig. 3a). However, as crop biomass is harvested every year, it is an ephemeral carbon stock, and thus the conversion of savanna to maize fields may result in substantial net carbon losses in the longer term (Woomer 1993). Furthermore, agricultural intensification may severely alter soil conditions in savannas, resulting in significant soil carbon losses (Williams et al. 2008). On the other hand, abandoned crop fields may regrow quickly and restore the lost aboveground carbon within ~25 years (Williams et al. 2008).

The strong reduction in total biomass from natural lower montane forests to agroforestry systems and grasslands at the same elevation indicates that land-use change in the lower montane zone results in considerable carbon losses (Fig. 3b). Tree reduction seemed to be the main driver for these losses, and traditional home gardens and coffee plantations still stored 26% and 16% of the natural forests' biomass, respectively, while mainly treeless grasslands retained only 1% of the forest biomass. Not all vegetation strata were negatively affected. For example, home gardens had a higher biomass in the shrub layer than natural forests and coffee plantations. This was due to the high density of banana plants, which are short-lived and hence, also constitute an ephemeral carbon stock. Accordingly, home gardens store higher amounts of carbon than traditional grasslands, but not than shaded coffee plantations. This supports conclusions that carbon stocks in agricultural landscapes depend largely on the abundance and size of woody plants (for reviews, see Albrecht and Kandji 2003, Luedeling et al. 2011).

Past selective logging of large individual trees neither affected the current total biomass of montane *Ocotea* forests, nor did it significantly affect the biomass of the different strata (Fig. 3c). In accordance with our results, Medjibe et al. (2011) found that selective logging and thinning of trees does not strongly affect carbon stocks in central African lowland forests and Gourlet-Fleury et al. (2013) found a full recovery of aboveground biomass after selective logging within 24 years. At Mt. Kilimanjaro, selective logging mainly concerned the commercially important camphor tree (*Ocotea usambarensis*) and the logging activities in this zone occurred ~30–60 years ago. However, although biomass may recover quickly, selectively logged forests may still continue to differ in their structure, species richness and composition (Marín-Spiotta et al. 2007, Martin et al. 2013, Rutten et al. 2015).

Conclusions

The coinciding unimodal elevation patterns of aboveground biomass and precipitation suggest that biomass is mainly driven by precipitation at Mt. Kilimanjaro. As tree biomass contributed 98% of total biomass in forest habitats, shrub and herb biomass may be largely neglected for forests, if conserving carbon stocks is the only interest. However, in open habitats, such as

savannas, shrub biomass can exceed tree biomass and thus, leaving out the shrub layer in inventories will clearly fail to produce accurate estimates of aboveground carbon stocks. Compared with tree biomass, herbaceous biomass followed an inverse elevation pattern and played a considerable role in open habitats, particularly in the higher subalpine and alpine vegetation.

Biomass stocks were highest in the montane forest belt that mostly lies inside Mt. Kilimanjaro National Park. Consequently, truly protecting these forests together with the forest remnants in the lower montane area and the savannas is by far the most effective means of reducing carbon emissions due to deforestation in this zone. This is underlined by our finding that upper montane *Podocarpus* forests on Mt. Kilimanjaro store considerably more carbon than forests at similar elevations on other continents. Our study furthermore provides first estimates of afro-alpine carbon stocks.

We showed that the transformation of savannas into intensive maize fields and of natural lower montane forests into agricultural landscapes is a major cause of aboveground carbon loss on Mt. Kilimanjaro. However, multi-layered agroforestry systems, such as the traditional home gardens, can still store up to a quarter of the carbon of the natural forests, underlining the importance of agroforestry for maintaining carbon stocks. Furthermore, we showed that land use differently affects the different vegetation strata and can substantially change the proportion of woody and non-woody components in an ecosystem. This may be important for other ecosystem properties, such as productivity, soil formation and biodiversity.

Tanzania was chosen for a pilot study for calculating REDD+ opportunities to prevent carbon losses in developing countries (Burgess et al. 2010). In this context, Mt. Kilimanjaro provides an excellent example of a mountain densely populated up to around 2000 m and with a prominent role for regional timber and water supply (Agrawala et al. 2003). Protecting the forest in the national park above about 2000 m and maintaining large shading trees in home gardens and coffee plantations at lower elevations, along with protecting the few lower montane forest remnants and the savanna remnants, may therefore be the most effective way of minimizing carbon losses due to land-use intensification at this mountain.

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Supplemental Material

Appendix A

Table A1. Overview over biomass and carbon stocks of the 55 study plots, their location (Zone), whether they are anthropogenically affected (Status), elevation, and climate type.

	Plot characteristics					Biomass (Mg ha^{-1})				
ID	Zone	Status	Plot	Elevation (m)	Climate type	Herbs	Shrubs	Trees	Total	Total carbon (Mg C ha^{-1})
1	Savanna	Natural	SAV1	871	Dry	1.77	4.9	7.3	14.0	6.8
2	Savanna	Natural	SAV2	906	Dry	1.35	7.3	3.1	11.7	5.6
3	Savanna	Natural	SAV3	1153	Dry	2.17	0.4	1.3	3.9	1.9
4	Savanna	Natural	SAV4	984	Dry	2.35	2.9	2.2	7.5	3.6
5	Savanna	Natural	SAV5	951	Dry	4.95	6.5	3.6	15.0	7.2
6	Savanna	Affected	MAI1	1009	Dry	14.78	0	0.1	14.9	7.2
7	Savanna	Affected	MAI2	866	Dry	24.75	0	0	24.8	11.9
8	Savanna	Affected	MAI3	886	Dry	17.53	0	0.1	17.6	8.5
9	Savanna	Affected	MAI4	960	Dry	9.06	0	0.6	9.6	4.6
10	Savanna	Affected	MAI5	920	Dry	9.78	2.9	3.4	16.2	7.8
11	Low.mon	Natural	FLM1	1920	Wet	1.63	3.8	157.1	162.5	78.3
12	Low.mon	Natural	FLM2	1800	Wet	0.3	5.6	229.1	235.0	113.3
13	Low.mon	Natural	FLM3	1560	Wet	1.4	7.9	433.5	442.8	213.4
14	Low.mon	Natural	FLM4	1623	Wet	0.65	2.5	661.2	664.3	320.2
15	Low.mon	Natural	FLM6	2040	Wet	0.74	3.7	296.2	300.6	144.9
16	Low.mon	Affected	HOM1	1647	Wet	1.05	32.1	98.6	131.8	63.5
17	Low.mon	Affected	HOM2	1169	Moist	0.41	20.5	113.3	134.3	64.7
18	Low.mon	Affected	HOM3	1788	Wet	1.04	12.8	59.4	73.2	35.3
19	Low.mon	Affected	HOM4	1275	Moist	0.59	18.8	61.1	80.5	38.8
20	Low.mon	Affected	HOM5	1560	Moist	0.29	29.6	16.5	46.4	22.4
21	Low.mon	Affected	COF1	1306	Moist	1.48	7.6	135.9	145.0	69.9
22	Low.mon	Affected	COF2	1345	Wet	2.99	2.1	27.1	32.2	15.5
23	Low.mon	Affected	COF3	1305	Moist	0.83	2.5	27.6	30.9	14.9
24	Low.mon	Affected	COF4	1124	Moist	1.24	2.7	26.4	30.25	14.6
25	Low.mon	Affected	COF5	1648	Moist	1.47	32.3	17.7	51.4	24.8
26	Low.mon	Affected	GRA1	1660	Wet	7.03	0	0	7.0	3.4
27	Low.mon	Affected	GRA2	1748	Wet	1.33	0.3	0	1.7	0.8
28	Low.mon	Affected	GRA3	1485	Moist	2.39	0	1.3	3.7	1.8
29	Low.mon	Affected	GRA4	1312	Moist	1.69	0.2	1.5	3.4	1.7
30	Low.mon	Affected	GRA5	1303	Moist	1.84	0	0	1.8	0.9
31	Montane	Natural	FOC1	2120	Wet	1.31	7.8	376.0	385.0	185.6
32	Montane	Natural	FOC2	2260	Wet	1.58	10.0	378.6	390.2	188.1
33	Montane	Natural	FOC3	2540	Wet	0.82	9.0	274.7	284.5	137.1
34	Montane	Natural	FOC4	2650	Wet	0.9	2.2	204.5	207.6	100.0
35	Montane	Natural	FOC5	2750	Wet	1.11	1.1	138.4	140.6	67.8
36	Montane	Affected	FOD1	2220	Wet	0.77	9.3	354.3	364.4	175.6
37	Montane	Affected	FOD2	2470	Wet	1.83	2.3	280.6	284.7	137.2
38	Montane	Affected	FOD3	2270	Wet	1.85	3.9	351.2	356.9	172.0
39	Montane	Affected	FOD4	2560	Wet	1.47	5.4	353.0	359.8	173.4

Table A1. Continued.

ID	Plot characteristics			Elevation (m)	Climate type	Biomass (Mg ha^{-1})				Total carbon (Mg C ha^{-1})
	Zone	Status	Plot			Herbs	Shrubs	Trees	Total	
40	Montane	Affected	FOD5	2370	Wet	0.76	24.4	398.7	423.9	204.3
41	Upp.mon	Natural	FPO1	2850	Wet	3.08	3.6	372.0	378.7	182.5
42	Upp.mon	Natural	FPO2	2940	Wet	1.9	...	...	...	...
43	Upp.mon	Natural	FPO3	2970	Wet	1	...	...	...	...
44	Upp.mon	Natural	FPO4	2720	Wet	4.04	0	370.0	374.1	180.3
45	Upp.mon	Natural	FPO5	2800	Wet	9.76	1.8	352.7	364.2	175.5
46	Sub.alpine	Natural	FER0	3880	Moist	16.73	...	...	...	...
47	Sub.alpine	Natural	FER1	3849	Moist	7.16	...	...	...	...
48	Sub.alpine	Natural	FER2	3510	Moist	6.47	...	...	...	...
49	Sub.alpine	Natural	FER3	3830	Moist	4.3	...	...	...	...
50	Sub.alpine	Natural	FER4	3500	Moist	9.48	...	...	...	...
51	Alpine	Natural	HEL1	3880	Dry	13.54	0	0	13.5	6.5
52	Alpine	Natural	HEL2	4190	Dry	7.27	0	0	7.3	3.5
53	Alpine	Natural	HEL3	4240	Dry	1.25	0	0	1.3	0.6
54	Alpine	Natural	HEL4	4390	Dry	4.29	0	0	4.3	2.1
55	Alpine	Natural	HEL5	4550	Dry	5.3	0	0	5.3	2.6

Notes: Biomass and carbon stocks are scaled up to a one hectare standard. Zone abbreviations are: Savanna zone (Savanna), lower montane zone (Low.mon), montane zone (Montane), upper montane zone (Upp.mon), subalpine zone (Sub.alpine) and alpine zone (Alpine). Plot abbreviations are: savanna woodlands (SAV), maize fields (MAI), lower montane rainforest (FLM), home gardens (HOM), coffee plantations (COF), grasslands (GRA), montane *Ocotea* forests (FOC), selectively logged *Ocotea* forests (FOD), upper montane *Podocarpus* forests (FPO), subalpine *Erica* forests (FER), alpine *Helichrysum* heathlands (HEL). Elevation is the plot elevation in m a.s.l. and Climate type indicates in which category of Chave et al. (2005) the plots were assigned according to temperature and precipitation patterns (Appendix B).

Appendix B

Choice of the allometric equations

The pantropical allometric equations developed by Chave et al. (2005) have been widely applied for natural and disturbed tropical forests across all continents (e.g., Djomo et al. 2010, Preece et al. 2012, Rutishauser et al. 2013), and estimates were found not to be significantly biased compared with actual biomass values or locally developed equations (Vieilledent et al. 2012, Fayolle et al. 2013). Several of these studies were conducted in tropical Africa (e.g., Djomo et al. 2010, Fayolle et al. 2013), confirming the utility of the approach for Africa, although no samples from Africa had been used by Chave et al. (2005) when developing the models. We assigned our plots according to their local temperature and precipitation to the categories "dry forest", "moist forest" and "wet forest" as used by Chave et al. (2005) (Table B1, Appendix A). These categories are based on the ratio between mean annual temperature (MAT) and mean annual precipitation (MAP) with MAT: MAP between 1:25 and 1:50 corresponding to dry forest (subhumid), between 1:50 and 1:100 to moist forest (humid) and $<$ 1:100 to wet forest (per-humid).

Kuyah et al. (2012) showed that Chave's "dry forest" equation estimated the biomass of East African agroforestry systems in humid conditions with a mean error of 5%, whereas the "moist forest" equation estimated it with 25% error. Therefore, we also used the dry forest equation for the three agriculturally used land cover types of the lower montane zone (home gardens, coffee plantations and grasslands), although climatically they would be assigned to the "moist forest" conditions. To test whether this use of the dry forest equation affected our results, we repeated our analyses with the moist forest equation and found that it did not change our conclusions concerning the differences between land cover types in the lower montane zone, although it yielded somewhat higher tree biomass estimates. Furthermore, it has been recently shown that crown diameter may be an additional crucial parameter improving allometric biomass estimates (Goodman et al. 2014). Although data on crown diameter was available for our trees, it could not be implemented, as there is currently no pantropical equation including crown size available with a reasonable sample size across

Table B1. Allometric equations used for estimating aboveground biomass stocks of trees and shrubs in different habitats on Mt. Kilimanjaro.

Authors	Type	Equation
Chave et al. 2005	Dry forest	$AGB = \exp(-2.187 + 0.916\ (\ln(wd \times dbh^2 \times H)))$
Chave et al. 2005	Wet forest	$AGB = \exp(-2.557 + 0.940\ (\ln(wd \times dbh^2 \times H)))$
Schnitzer et al. 2006	Lianas	$AGB = \exp(-1.484 + 2.657\ (\ln(dbh)))$
Hairiah et al. 2010	Bananas	$AGB = 0.03 \times dbh^{2.13}$
Hairiah et al. 2010	Coffee	$AGB = 0.281 \times dbh^{2.06}$
Mugasha et al. 2013	Savannas	$AGB = 0.0763 \times dbh^{2.2046} \times H^{0.4918}$

Notes: Parameter used for the equations are: wood density (wd; dry weight divided by fresh volume), diameter at breast height (dbh) and total plant height (H).

continents (Goodman et al. 2014). For lianas we used the pantropical equation by Schnitzer et al. (2006) (Table B1).

The biomass of banana plants and regularly pruned coffee plants in coffee plantations and home gardens was obtained using the equations recommended by Hairiah et al. (2010), all using dbh as the only input variable (Table B1).

Savanna trees in this study were generally very small in diameter and the Chave equations have been shown to be less precise for small diameter trees (van Breugel et al. 2011). Therefore, we adopted a more recent equation for the trees in the savanna zone (SAV, MAI; Appendix A), which was especially developed by Mugasha et al. (2013) for savanna and Miombo woodlands in Tanzania (Table B1). Mugasha et al. (2013) developed their equations based on destructive sampling over four savanna regions across Tanzania and also showed that the Chave "dry forest" equation underestimated the aboveground biomass of the Miombo woodlands with an error of 11%.

Overall, we are confident that we applied the most reliable equations to estimate biomass for the habitats of our study.